

## Host range and some properties of *Physalis mosaic virus*, a new virus of the turnip yellow mosaic virus group

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### Abstract

An apparently undescribed virus was isolated from *Physalis subglabrata* in Illinois, USA, and its properties were studied. The virus was named *Physalis mosaic virus* (PMV). It was readily transmitted by sap inoculation to 23 out of 34 Solanaceae tested, to *Chenopodium foetidum* and *Sonchus oleraceus* but not to 28 other non-solanaceous species inoculated. Purified preparations of PMV contained isometric particles of 27 nm in diameter, which sedimented as two components with sedimentation coefficients of 50 and 112 S. The 112 S component was infectious, the 52 S component was not. The virus contained 38% ribonucleic acid with a molar base content of G 14.4%, A 22.9%, C 37.2% and U 25.5%.

Purified preparations were highly infectious; a concentration of about 6000 particles per ml was infectious on plants.

PMV is a member of the Andean potato latent virus subgroup of the turnip yellow mosaic virus group. The virus was closely related to the viruses: Andean potato latent, belladonna mottle, dulcamara mottle and egg-plant mosaic.

### Introduction

Plants of *Physalis subglabrata* showing an interveinal chlorosis or, and mosaic on some leaves, were found on roadsides south of Urbana, Illinois, USA. A virus from such plants was transmitted by sap to several plant species, among them healthy plants of *P. subglabrata* which then developed either a systemic mosaic or a mottling. The virus is named *Physalis mosaic virus*.

This paper describes the results of experiments conducted at Wageningen. They involved studies on some properties, particularly those which may be useful for distinguishing the virus from serologically related viruses of the turnip yellow mosaic group.

### Materials and methods

The virus was maintained in *Datura stramonium* and *Nicotiana clevelandii*. The stock culture and all test plants were kept in insect-free glasshouses at 18-23°C. Back inoculations were made to *N. clevelandii* or *D. stramonium*.

Preparations of high purity were obtained by the following procedure. Infected leaves (*N. clevelandii*) were triturated in 3 to 4 times their weight of 0.1 M glycine buffer containing 0.01 M magnesium chloride, pH 7.0. After filtration through cheesecloth, butanol (8%) was added to the extract. The emulsion was centrifuged the

next day at 10,000 g for 10 min. The virus preparation was then frozen at  $-18^{\circ}\text{C}$ , thawed the next day, and centrifuged again at low speed. The virus could be further purified by one cycle of differential centrifugation at 100,000 g for three hour and 10,000 g for 10 min.

Sucrose density gradient columns (3–30% sucrose) were prepared in 0.1 M glycine buffer (pH 7.0) containing 0.01 M  $\text{MgCl}_2$ . After centrifugation (53,500 g for two hour) the tubes were monitored by passage through an LKB Uvicord analyser.

Sedimentation analyses were made in a Spinco Model E analytical ultracentrifuge, using Schlieren optics. Sedimentation coefficients were calculated by Markham's (1960) graphical method.

The nucleotide composition of the virus was estimated as described by Knight (1963). Preparations either of complete virus or of phenolextracted nucleic acid, were hydrolyzed with 1 N HCl at  $100^{\circ}\text{C}$  for one hour. The nucleotides and purines were separated chromatographically on Whatman No 1 paper using a solvent containing 70 ml t-butanol, 7.8 ml 10 N HCl and 22.2 ml water.

Antiserum to *Physalis* mosaic virus (PMV) was prepared in rabbits by giving three intramuscular injections of 2 ml virus emulsified with Freund's incomplete adjuvant, on three occasions at intervals of two weeks. The virus concentration was about 5 mg/ml. Serological tests were conducted in agar gel-diffusion plates using 2% Difco Noble agar; six wells surrounded the central well (centre to centre) at a distance of 6 mm. The micro-precipitin test was used under paraffin-oil. Antisera against Andean potato latent virus (APLV), belladonna mottle virus (BMV), dulcamara mottle virus (DMV), and egg-plant mosaic virus (EMV) were kindly supplied by R. Bercks.

In cross protection tests *N. glutinosa* plants were inoculated with APLV and DMV. After the appearance of systemic symptoms, the plants were superinoculated with PMV. In addition *N. glutinosa* was first inoculated with PMV, and 9 days later superinoculated with either APLV or DMV. The effect of super-inoculation was studied visually and by back inoculations to *N. tabacum* 'White Burley' and *Petunia hybrida* 'Pink Beauty'.

Preparations were examined in a Siemens Elmiskop I electron microscope after contrasting with neutral 2% (w/v) phosphotungstate.

To measure the virus concentration, an assumed absorbance coefficient of  $8.5 \text{ mg}^{-1} \text{ ml}^{-1} \text{ cm}^{-1}$  (at 260 nm) was used.

## Results

*Host range and symptoms.* The host range of PMV appeared to be almost restricted to the Solanaceae. *Capsicum annuum* produced light green spots on the inoculated leaves within 11 days and a systemic mottling within 18 days. Necrotic local lesions were produced in *Datura bernhardii* and *D. metel* and chlorotic and some necrotic local lesions in *D. stramonium*; later these species produced a systemic mosaic, often with some necrotic lesions. A systemic mosaic was induced in *Nicandra physaloides* after 11 days. Necrotic local lesions developed in *Nicotiana benthamiana*, *N. clevelandii*, *N. debneyi*, *N. glutinosa*, *N. megalosiphon*, *N. rustica*, *N. sylvestris*, *N. tabacum* 'Samsun', 'Samsun NN' and 'White Burley'. In *N. clevelandii* local lesions were followed by a systemic mottling. No symptoms were recorded on *N. virginiana*, *P. hybrida* 'Pink Beauty', and *Solanum pseudocapsicum*, but the virus could be recovered from these

species. Chlorotic and necrotic local lesions, later followed by mosaic, occurred in *Physalis floridana*, *P. ixocarpa*, *P. peruviana* and *P. subglabrata*. During later stages of infection, a vein necrosis and a necrosis of the top leaves was sometimes noticed in *P. subglabrata*.

In all species with systemic infection, mosaic or mottling was often accompanied by veinbanding or veinclearing. These symptoms in combination were in some cases difficult to classify.

*Chenopodium foetidum* and *Sonchus oleraceus* were the only susceptible species found outside the Solanaceae. *C. foetidum* reacted with systemic chlorotic spots, sometimes later becoming necrotic. No symptoms were recorded on *S. oleraceus*, but the virus could be recovered from this species.

The following species were found not to be infected: Amaranthaceae: *Celosia argentea*, *Gomphrena globosa*; Apocynaceae: *Vinca rosea*; Chenopodiaceae: *Beta vulgaris* 'Corona', *Chenopodium amaranticolor*, *C. quinoa*; Compositae: *Callistephus chinensis* 'plenus' 'Madeleine', *Chrysanthemum indicum* 'Indianapolis', *Dahlia variabilis*, *Helianthus annuus*, *Lactuca sativa* 'Blackpool', *Zinnia elegans*; Cruciferae: *Brassica pekinensis*, *Raphanus sativus* 'Ronde, rode broei'; Cucurbitaceae: *Cucumis melo* 'Cantaloup de Bellegarde', *Cucumis sativus* 'Sporu'; Gramineae: *Hordeum vulgare* 'Cambrinus', *Triticum aestivum* 'Stella'; Leguminaceae: *Glycine soja*, *Medicago sativa*, *Ononis spinosa*, *Phaseolus vulgaris* 'Masterpiece' and 'Prince', *Pisum sativum* 'Onward', *Trifolium incarnatum*, *Trifolium repens*, *Vicia faba* 'Hedosa', *Vigna sinensis* 'Blackeye'; Solanaceae: *Atropa belladonna*, *Solanum andigenum*, *S. chacoense*, *S. demissum*, *S. dulcamara*, *S. melongena*, *D. nigrum*, *S. phureja*, *S. stoloniferum*, *S. tuberosum* 'Eigenheimer', *S. verrucosum*; Umbelliferae: *Daucus carota* 'Amsterdamse bak'.

*Properties in crude sap and leaf material.* Sap from systemically infected *N. clevelandii* was still infectious at a dilution of  $10^{-8}$ .

Lyophilized plant (*D. stramonium*) material was still infectious after 2.5 years. Frozen leaf material, stored at  $-18^{\circ}\text{C}$ , was still infectious after two months. Purified suspensions were infectious for 50 days when stored at about  $3^{\circ}\text{C}$ .

*Properties of purified preparations.* Purified preparations centrifuged on sucrose density gradient columns for two hour at 53,500 g formed two light-scattering zones. Only the bottom zone was infectious. Both were serologically active.

These preparations contained two components with sedimentation coefficients (S 20°, W) of 112 S and 50 S. These values are very close to those of 113 S and 53 S obtained for BMV (Paul, 1971), those of 111 S and 53 S obtained for EMV (Gibbs and Harrison, 1969) and those of other members of this subgroup (Gibbs et al., 1966). The 112 S component always accounted for the larger peak. The sedimentation coefficients of the component of PMV suggest (Reichmann, 1965) that the 112 S component contains 38% nucleic acid, a value also close to that reported for the other members of this group.

The absorption spectrum of purified virus with a maximum at 260 nm and a minimum at 240 nm was typical of a nucleoprotein with a high nucleic acid content. The 260:280 and 260:240 absorption ratios were 1.60 and 1.37. The nucleic acid had maximum and minimum absorption at 260 nm and 235 nm with 260:280 and 260:235 absorption ratios of 1.67 and 1.75 (Fig. 1). The high proportion of cytidylic acid and

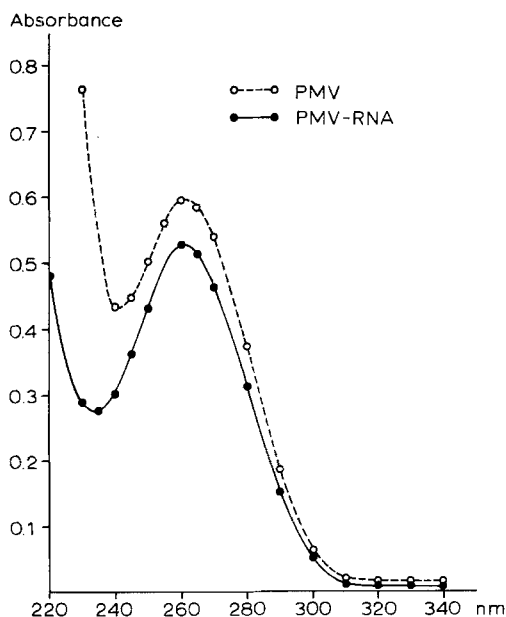


Fig. 1. The u.v. absorption of *Physalis* mosaic virus (PMV) and its nucleic acid.

Fig. 1. De absorptie van *Physalis*-mozaïek-virus en zijn nucleïnezuur in het ultraviolette gebied.

low proportion of guanine accounts for the minimum at 235 nm and the low value found for  $E_{\max}/E_{\min}$  and  $E_{260}/E_{280}$  (Table 1, Fig. 1).

The base composition obtained in 26 analyses are given in Table 1. Compared to the values found for the other viruses of the turnip yellow mosaic virus group the content of guanine and uracil was slightly lower and the cytosine content higher in PMV. Despite these differences the base composition of PMV shows the specific pattern of base composition characteristic of this group. The ratio between the purine and pyrimidine bases is 0.59; a ratio that has also been found for APLV, EMV, *Ononis* yellow mosaic virus (OYMV), and *Scrophularia* mottle virus (ScMV) (Bercks et al., 1971). This ratio is higher for BMV, DMV and turnip yellow mosaic virus (TYMV).

Table 1. Molar base ratio of PMV and other members of the turnip yellow mosaic virus group.

Virus	Moles (%)				Source
	guanine	adenine	cytosine	uracil	
PMV	14.4	22.9	37.2	25.5	this study
APLV	15.2	21.6	34	29.2	Gibbs et al., 1966
BMV	17.5	22.8	32.8	26.9	Paul, 1971
DMV	16.7	22.6	32.3	28.5	Gibbs et al., 1966
EMV	16.3	21.0	38.2	24.8	Bercks et al., 1971
OYMV	15.6	21.0	34.2	29.4	Gibbs et al., 1966
ScMV	16.2	21.4	32.7	29.3	Bercks et al., 1971
TYMV	17.2	22.4	38.3	22.1	Matthews, 1970

Tabel 1. De verhouding van de basen in het ribonucleïnezuur van het *Physalis*-mozaïekvirus en andere leden van de 'turnip yellow mosaic virus' groep.

Table 2. Titres of antisera of *Physalis* mosaic virus (PMV) and other members of the turnip yellow mosaic virus group obtained in agar gel-diffusion and microprecipitin tests with PMV.

Test	PMV	APLV (1024)*	BMV (128)	DMV (512)	EMV (2048)
Microprecipitin	256	256	64	64	256
Agar gel-diffusion	64	64	16	8	64

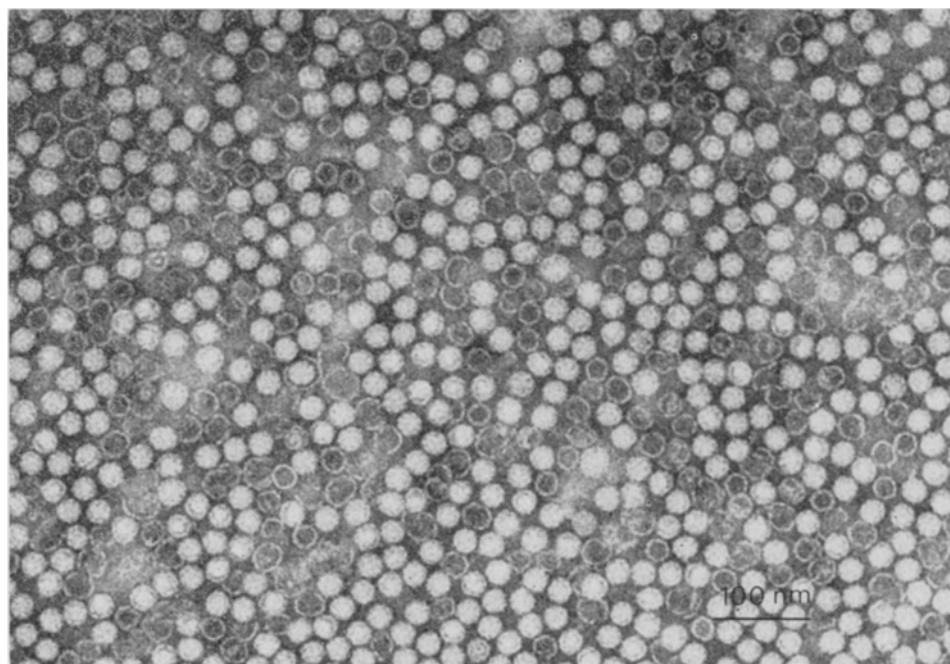
\* In brackets the homologous titres as determined by Bercks (personal communication).

*Tabel 2. Titers van antisera tegen het Physalis-mozaïekvirus (PMV) en andere leden van de 'turnip yellow mosaic virus' groep, zoals die in de microprecipitatietoets en de agar geldiffusietoets met PMV werden bepaald.*

The virus is serological related to APLV, BMV, DMV, and EMV (Table 2). PMV did not precipitate with antisera prepared against TYMV.

When mounted in PTA the particles were about 27 nm in diameter with a regular polygonal outline (Fig. 2). Between 20 and 35% of the particles were penetrated by PTA. In some of the particles a substructure could be revealed which was identical to that of BMV (Paul et al., 1968), of EMV (Gibbs and Harrison, 1969), of ScMV (Bercks et al., 1971) and the viruses of the APLV group (Gibbs et al., 1966).

Fig. 2. Electron micrographs showing PMV particles mounted in neutral phosphotungstic acid. Bar represents 100nm.



*Fig. 2. Elektronenmicroscopische opname van Physalis-mozaïekvirus (PMV) dat met neutraal wolframzuur werd gecontrasteerd. Maatstreepje duidt 100 nm aan.*

*Infectivity of purified preparations.* Tenfold dilutions were made of a preparation containing  $5.3 \times 10^{-3}$  g virus/ml, to  $10^{-12}$ . Each dilution in a quantity of 0.5 ml was tested for infectivity on 10 *N. clevelandii* plants. All the dilution up to  $10^{-11}$  appeared to be infectious. Assuming a particle weight of  $5.3 \times 10^6$ , which is the mean of the value for BMV ( $5.2 \times 10^6$ ; Paul, 1971) and TYMV ( $5.4 \times 10^6$ ; Matthews, 1970) it can be calculated that 6000 particles/ml are necessary to infect a plant systemically. For *D. stramonium* the minimal infective dose proved to be  $6 \times 10^6$  particles/ml inoculum.

*Cross protection tests.* Tests were made to investigate whether plants systemically infected with APLV and DMV resisted infection with PMV. On leaves of *N. glutinosa* plants, with a systemic chlorotic mosaic (Gibbs et al., 1966) of APLV and DMV, and super-inoculated with PMV, local lesions of PMV appeared seven days after inoculation whereas they were visible within five days on the unchallenged plants. On back inoculation to *N. tabacum* 'White Burley' a noticeably smaller number of local lesions were produced when inoculated with sap from the challenged plants than with sap from those with PMV only. The delay in local lesion formation on *N. glutinosa* and the reduced number of local lesions on 'White Burley' indicate a weak cross protection between PMV and both APLV and DMV.

A weak resistance was also observed when the reciprocal inoculations were made on *N. glutinosa*. APLV and DMV, super-inoculated on the PMV-inoculated leaves, did not cause the formation of local lesions on these leaves such as occurred on the control plants. A severe mosaic appeared after 10 days on the control plants and a weak mosaic after 13 days on the challenged plants. The reaction on *Petunia* was positive for the controls and negative for the challenged plants, indicating a lower amount of APLV and DMV in these plants.

## Discussion

The virus described has a number of properties in common with many of the viruses allied to TYMV. The particles are of two types with sedimentation coefficients of 112 and 50 S, and have morphology, size and base composition comparable to those of the other members of the turnip yellow mosaic virus group.

PMV is serologically related to APLV, BMV, DMV and EMV, which are all grouped in the Andean potato latent virus subgroup (Gibbs et al., 1966). The relation of this virus to OYMV and the more recently described members such as *Desmodium* yellow mottle virus (DYMV) (Walters and Scott, 1972), *Plantago* mottle virus (PIMV) (Granett, 1973), and SrMV has not been studied. As these viruses are also serologically related to APLV, BMV, DMV and EMV, it can be safely assumed that PMV is also related to them.

So far serology has been an important criterion in grouping plant viruses and classifying subgroups. However, serology seems of relative unimportance in differentiating viruses within morphological groups because only a small part of the total genetic information in the virus genome is translocated in phenotypic properties studied by serology (Bos, 1970). Thus nucleic acid properties may be of more interest, and Gibbs et al. (1966) determined base composition to differentiate the APLV subgroup. But genetic information is mainly determined by base sequence. Hence, Swaans and Van Kammen (1973) advocated application of molecular hybridization. They con-

Table 3. Differential host range for APLV, BMV, DMV, EMV, OYMV, and PMV.

Host	Virus					
	APLV	BMV	DMV	EMV	OYMV	PMV
<i>Pisum sativum</i>	—	—	—	?	S*	—
<i>Nicotiana glutinosa</i>	l + s	l + s	l + s	l + s	—	l
<i>N. tabacum</i> 'White Burley'	(1)	s	—	l + s	—	l
<i>Solanum melongena</i>	(s)	s	?	s	?	—
<i>S. tuberosum</i>	s	—	—	s	?	—
<i>Atropa belladonna</i>	—	+	—	—	—	—

\*s = systemic infection, l = local infection, ( ) symptomless infection, — = no infection shown or recorded, ? = not tested. The results given are compiled from observations by Gibbs et al. (1966), Paul et al. (1968), Gibbs and Harrison (1969) and the present authors.

Tabel 3. Een reeks planten waarop leden van de 'Andean potato latent virus' subgroep kunnen worden onderscheiden.

cluded the Vs and Nig isolates of cowpea mosaic virus to be different viruses rather than strains of one virus because of biological differences, weak serological relationships and, as shown by Van Kammen and Rezelman (1972), no homology in nucleotide sequences. Such research may be required to further elucidate the more exact relationships between members of the TYMV group and its subgroup discussed here.

PMV clearly differs from OYMV that the former does not infect Leguminaceae. With APLV, BMV, DMV, and EMV it shares most of its experimental hosts among solanaceous species. A host range to distinguish these viruses and to isolate or separate them is given in Table 3. APLV and EMV infect wild and cultivated potatoes, but BMV, DMV and PMV do not. Of the plants susceptible to BMV only *Atropa belladonna* and *Solanum melongena* were not susceptible to PMV indicating a close relationship between these viruses.

Using serological tests, Gibbs et al. (1966) did not find cross reactions between APLV, DMV, and OYMV. However, approaching this problem with APLV, DMV, and PMV by using differential and assay hosts we found some retardation in symptom development and a lower concentration of the super-inoculated virus in the challenge-inoculated plants than in the comparable control plants. Our results indicated that plants which had already been infected with one of these viruses were slightly resistant to super-infection.

Gibbs et al. (1966) grouped APLV, DMV, and OYMV as the Andean potato latent subgroup of the turnip yellow mosaic virus group. EMV, ScMV, DYMV and PIMV have also been included in this subgroup on serological grounds. Of these viruses EMV was the first to be described (Ferguson, 1951) and for priority reasons it may be preferable to call this subgroup the eggplant mosaic virus group.

## Samenvatting

*De waardplantenreeks en een aantal eigenschappen van het Physalis-mozaïekvirus, een nieuw virus van de 'turnip yellow mosaic virus' groep*

Een nog niet eerder beschreven virus, dat in de staat Illinois (V.S. van Amerika) op *Physalis subglabrata* was gevonden, werd in Wageningen bestudeerd. Het virus dat

'*Physalis mosaic virus*' (PMV) (in het Nederlands: *Physalis*-mozaïekvirus) werd genoemd, kon met sap worden overgebracht.

Behalve *Chenopodium foetidum* en *Sonchus oleraceus* bleken ook 23 van de 34 getoetste soorten uit de familie Solanaceae vatbaar voor dit virus te zijn. Gezuiverde virus preparaten bevatten isometrische deeltjes met een diameter van 27 nm (Fig. 2). Het virus bestaat uit twee deeltjes met sedimentatie-coëfficiënten van 112 en 50 S. Het 112 S deeltje bleek infectieus te zijn, het andere niet. Op grond van de sedimentatiecoëfficiënten kan worden berekend dat het 112 S deeltje 38% nucleïnezuur bevat. Voor de basenverhouding in het nucleïnezuur werd 22,9% adenine, 14,4% guanine, 37,2% cytosine en 25,5% uracil gevonden (Tabel 1). Het hoge gehalte van cytosine kwam ook tot uiting in de U.V. absorptiekromme van het virus en het nucleïnezuur (Fig. 1). Het gezuiverde virus bleek zeer infectieus te zijn; 6000 deeltjes/ml waren in staat een plant van de soort *Nicotiana clevelandii* ziek te maken.

Op grond van serologisch onderzoek kon het virus tot de turnip yellow mosaic virus groep worden gerekend. Het vertoonde serologische verwantschap met de 'Andean potato latent virus' (APLV) subgroep (Tabel 2). In premunitieproeven bood het slechts een geringe bescherming tegen APLV en 'dulcamara mottle virus'. Het omgekeerde werd eveneens geconstateerd. De leden van de APLV-subgroep kunnen op grond van hun waardplantenreeks van elkaar onderscheiden worden (Tabel 3).

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### Note (added in proof)

In a recent paper Moline and Fries (Phytopathology 64 (1974) 44–48) described the recovery of a virus from *Physalis heterophylla* in Iowa. This virus had an almost identical host range to that of PMV described in this paper and had many properties common to the turnip yellow mosaic virus group. The authors identified this virus as a *Physalis* mottle strain of BMV to which it is serologically related. The serological relationships to other viruses such as APLV, DMV, EMV were not studied. The available data suggest that this virus and PMV may be closely related.

In another recent paper Koenig and Givord (Virology 58 (1974) 119–125) reported a study on the serological relationships in the turnip yellow mosaic virus group. They demonstrated a continuous range of serological relationships within the group and concluded that a subdivision into a turnip yellow mosaic and an Andean potato latent virus subgroup is not justified.

### Addresses

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## Book review

The Terminology Sub-Committee of the Federation of British Plant Pathologists: A guide to the use of terms in plant pathology. Commonwealth Mycological Institute, Kew, Surrey, England. Phytopathological Papers No 17, 1973: 55 pp. £ 1.30.

Terminology is not merely a hobby of linguists but one of the basic expedients in adequately describing objects and phenomena. Terms have to be continuously adapted to the current state of knowledge. Moreover, employment in specialized branches of plant pathology and in distant fields like plant breeding tends to lead to a divergent use of phytopathological terms. Moreover, terms and their meaning slightly vary in different languages. Hence, it must be greatly welcomed that the Terminology Sub-Committee of the Federation of British Plant Pathologists has prepared an up-to-date guide to the use of terms in plant pathology.

The terms have been listed alphabetically with ample cross reference to synonyms and related terms. Each term is concisely defined, mainly based on earlier definitions given in less extensive lists of the American Phytopathological Society (1940, 1943) and of the British Mycological Society (1950, 1953). In case of slight differences of opinion both are cited. Pitfalls, possible confusions, synonymy and near synonymy are clearly discussed with helpful references to further literature. Several subjects, such as resistance and related terms, nomenclature of organisms, taxonomic categories and virus cryptograms, are outlined in considerable but easily accessible detail.

The list has been carefully prepared. Of course, one can differ of opinion as to some definitions given, but the authors themselves (P. W. Talboys, C. M. E. Garrett, G. C. Ainsworth, G. F. Pegg and E. R. Wallace) recognised that for some words no one definition is likely to command universal acceptance. They have modestly called their publication 'a guide to the use of terms'.

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